American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N. Y. 10024

NUMBER 2488 MAY 9, 1972

Conspectus of Patagonian Fossil Penguins

By George Gaylord Simpson[1]

ABSTRACT

The known fossil penguins of Argentina are all from the Patagonia Formation, mostly from its basal part, in Chubut and Santa Cruz, probably early Miocene but possibly late Oligocene in age. They are here reviewed on the basis of collections in the American Museum of Natural History, the Museo Argentino de Ciencias Naturales, the Museo de La Plata, and the British Museum (Natural History), and of publications mostly by Florentino Ameghino. Four genera are accepted as valid: *Palaeospheniscus* Moreno and Mercerat, with four accepted species, *Chubutodyptes* Simpson, with one accepted species, *Paraptenodytes* Ameghino with three accepted species (one, *P. brodkorbi*, here new, of dubious reference to this genus), and *Arthrodytes* Ameghino, with one accepted species. Numerous other names proposed by Ameghino are reduced to synonymy. *Palaeospheniscus*, the most abundant genus, covers a considerable range in size, and its separable size groups are here considered species. The correct name for the largest size group, hitherto called *P. robustus*, is *P. wimani*, as the holotype of *robustus* belongs in *Paraptenodytes*. *Neculus* may be a valid spheniscid genus, but it is virtually undefinable at present. *Palaeoapterodytes* was based on an error and is unidentifiable. *Cruschedula*, *Cladornis*, and *Argyrodyptes* were not penguins. The average size of the Patagonian fossil penguins is decidedly smaller than the average for their mostly older known relatives from New Zealand, Australia, and Seymour Island, only *Arthrodytes grandis* being distinctly larger than the living emperor penguin. No Patagonian genus is surely known from any other region. The Patagonian fossil penguin fauna is richer than any other known, fossil or Recent, but it is possible that not all the species were strictly synchronous and sympatric.

[1] University of Arizona and the Simroe Foundation, Tucson; Curator Emeritus, the American Museum of Natural History.

INTRODUCTION

When Francisco Moreno and Alcide Mercerat in 1891 described the first fossil penguins to be made known from South America, Florentino Ameghino was already famous as the leading Latin American paleontologist. Moreno and Ameghino had earlier been on affectionately fraternal terms, and Moreno, as director of the recently founded Museo de La Plata, had there obtained positions for two of the three Ameghino brothers, Don Florentino as secretary-subdirector and Don Carlos as a technician and collector. However, Moreno and Don Florentino quarreled bitterly and parted as implacable enemies. No sooner had Moreno and Mercerat published the pioneer study of Argentine fossil penguins, including some collected by Don Carlos, than Don Florentino (Ameghino, 1891) issued a criticism of it so bitter as to be downright libelous. It is ironic that Ameghino, who positively raved about what he considered to be Moreno's errors, was later himself to be author of one of the most curious errors in the history of this very subject — the case of *Palaeoapterodytes*, discussed later in the present study.

Don Carlos continued to collect fossil penguins, among many other things, and in 1895 Don Florentino again published on the subject. Being then even more troubled than usual by finances, the Ameghinos sold their collection of fossil birds to the British Museum (Natural History) in March, 1896. Well over 300 specimens were included. Relatively few were penguins, but among them was one type, "*Palaeospheniscus*" *robustus*, the distant separation of which from all other relevant types had a curious sequel, as will appear below.

Later Don Carlos made still larger collections of fossil penguins, and these eventually passed into the somewhat changeably named national museum in Buenos Aires with the purchase of all collections finally left as the Ameghinos' personal property. Florentino Ameghino discussed or listed some of them in publications of 1898, 1899, and 1901. Finally in 1905 he published a definitive, excellently illustrated memoir that included all then known Argentine fossil penguins and also, at secondhand on the basis of Wiman's then recent publications (1905a, 1905b), those from Seymour Island, off the tip of the Antarctic peninsula.

A few other small and relatively unimportant collections had been made, for example 16 fossil bird bones, mostly of penguins, purchased in 1899 by the British Museum (Natural History) from a Mr. Damon, not otherwise identified. These were recorded as from the "Santa Cruz Beds. Monte Leone. Patagonia," but the penguins were certainly from the Patagonia Formation, which immediately underlies the Santa Cruz Formation in that vicinity. That collection was not studied until 1970, when I found that it

contributes little to the subject although adding some data on tibiotarsi and coracoids, which are among the less well-known bones of these fossil species.

The most important collection was made for the American Museum of Natural History in the region of Trelew and Gaiman, Chubut, by a party under my direction which also included Coleman S. Williams and Justino Hernández. That was made the basis of an extended study (Simpson, 1946), including a listing of all previously proposed taxa of Patagonian fossil penguins, with critical remarks on each but without formal classification or revision. The two principal compendia on fossil birds, Lambrecht (1933) and Brodkorb (1963) have listed the proposed taxa in formal classifications, with some remarks on taxonomy but without firsthand study.

It has been increasingly clear that Ameghino, following criteria current 65 to 80 years ago but now greatly modified, proposed far too many taxa. It has also become evident that even the modernized classification by Brodkorb (1963) still has doubtful or erroneous items. Dissatisfaction was brought to a point by the discovery that one of the most familiar names, *Palaeospheniscus robustus*, has been misapplied ever since its proposal in 1895 and that there is corresponding confusion of taxa and their relationship.

A full, formal classification is therefore here presented. This is not the definitive revision that still is needed but that will require more specimens and further study. It is hoped, however, that a clarification of present knowledge of this interesting and important fauna is achieved.

Aiding in the present work has been study of the British Museum (Natural History) collection, some of which had never been studied and none of which had been studied since 1895. Norms for variation within and between species have been improved not only by data on the extensive American Museum of Natural History collection but also by study of skeletons of Recent penguins in the same museum, in the Museum of Comparative Zoology (Harvard), and in a collection at the Simroe Foundation (Tucson) kindly presented by the South African Museum. Other extended background is provided by the fact that in recent years I have been able to study at firsthand all the fossil penguins known from Australia, New Zealand, Seymour Island, and South Africa, and to observe nine of the 17 living species in their natural habitats.

With a single exception, all the relevant type specimens have been unusually well illustrated, mostly in Ameghino (1905). Those illustrations were also copied (although less clearly) in Ameghino's collected works (1934) and are so widely available that re-illustration here is unnecessary. The one important specimen not hitherto adequately figured is the type

of "*Palaeospheniscus*" *robustus*, and it is illustrated in the present study.

All measurements herein are given in millimeters.

The following abbreviations are used for museums and their collections:

AMNH, the American Museum of Natural History, New York
(The largest single collection, mainly from the Second Scarritt Expedition to Patagonia, 1933.)

BM (NH), the British Museum (Natural History), London
(Part of the Ameghinos' collection, purchased in 1896, and a small collection purchased in 1899.)

MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires
(The bulk of the Ameghinos' collection.)

MLP, Museo de La Plata, La Plata
(All of Moreno and Mercerat's materials [various collectors] and some later specimens collected by Carlos Ameghino.)

Catalogue numbers have not been given to specimens in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," and Museo de La Plata. Use of those initials here in designation of types indicates that the presence of the specimen in the museum indicated has been verified. In each case the specimen can be identified by unnumbered labels and by the figures in Ameghino (1905). For each type (holotype, syntype, lectotype) a reference to Ameghino's figure is given here.

Acknowledgments

First acquaintance with specimens in Argentine museums was long ago facilitated by the late L. Kraglievich and M. Doello-Jurado in the Museo Argentino de Ciencias Naturales and the late A. Cabrera in the Museo de La Plata. The presence of types as of now has been kindly checked by Guillermo del Corro in Buenos Aires and Eduardo P. Tonni in La Plata. Restudy of some specimens in the American Museum of Natural History was permitted by Bobb Schaeffer and assisted by George O. Whitaker. Extensive unpublished notes and measurements made by me when employed by that Museum and left in its archives were released for my further use in the present study. Work in the British Museum (Natural History) was made possible by a travel grant from the Royal Society of London and facilitated by A. J. Charig, who also provided an excellent cast of BM(NH) A/591. The photographs of that cast were taken by the Bureau of Audiovisual Services of the University of Arizona. I was employed part time by that University while doing some of the work on this study. Except as noted for various museums in the United States, Argentina, and England, the work was done at the Simroe Foundation.

OCCURRENCE AND AGE

The holotype of *Palaeospheniscus gracilis* was recorded as from the Deseadan stage, the "pyrotheriense" of Ameghino, but as discussed below under that species it almost certainly was float from the considerably later but immediately overlying Patagonia Formation. *Cruschedula revola* and *Cladornis pachypus* were also recorded as from the Deseadan,[1] perhaps correctly, but they are not penguins although first mistaken for such. All the other fossil penguins known from Argentina are definitely from the Patagonia Formation as far as recorded.

The stated geologic origins of Ameghino's holotypes (Ameghino, 1905, and museum labels) are as follows:

"Guaranítico" (indicating what we now call Deseadan): 1 specimen.

"Patagónico" (Patagonia Formation) without further specification: 12 specimens.

"Patagónico inferior" (lower Patagonia): 6 specimens.

"Patagónico medio" (middle Patagonia): 1 specimen.

"Patagónico superior" (upper Patagonia): 2 specimens.

Stated localities were as follows:

Patagonia, without further specification: 1 specimen.

The Patagonian coast: 1 specimen.

The Gulf of San Jorge: 5 specimens.

Trelew: 7 specimens.

San Julián: 6 specimens.

Mouth of the Río Santa Cruz: 1 specimen.

La Cueva: 1 specimen.

Specimens labeled as from Trelew were almost certainly in the lower or basal Patagonia, although most of them are labeled simply as "Patagoníco," without specification of level. Most of the specimens from San Julián were also from the lower Patagonia and are so labeled. The supposed "Guaranítico" specimen was probably from Cabeza Blanca (see *Palaeospheniscus gracilis*, below).

The American Museum collection includes one specimen from Cabeza Blanca, found on the surface of the Deseadan beds but believed to be derived from the base of the Patagonia Formation. All the other specimens were in the lower or basal part of the Patagonia Formation on the south side of the Chubut River in the region of Trelew and Gaiman. (For

[1] A Deseadan age and stage have been sufficiently defined, using mammalian faunas as time markers, but a Deseado formation has not been clearly defined, and it is not established that all the beds recognizable as Deseadan by their faunas belong to a single rock unit or Deseado formation even within Patagonia.

geology and localities see Simpson, 1935.)

The Patagonia Formation is a thick and somewhat complex series of marine sediments in some localities overlying continental or littoral beds of the Colhuehuapian Stage and in other localities underlying continental Santacrucian beds. Although the Colhuehuapian and Santacrucian mammalian faunas are distinct, they are so similar that the intervening time, represented by at least a part of the Patagonia Formation, cannot be long, geologically speaking. There are disputed, unsolved problems as to possible subdivisions of the Patagonia Formation and its possible total span and local ages in various parts of its very extensive exposures. Nevertheless there is no evidence that the fossil penguins are of appreciably diverse ages.

In that connection attention must be given to the three specimens definitely recorded as not from the lower Patagonia. The holotype of *Palaeospheniscus intermedius* is labeled as from the "Patagónico superior" of the vaguely designated "Golfo de San Jorge." However, that species is indistinguishable (in my opinion) from *Palaeospheniscus patagonicus*, the commonest species in the lower Patagonia Formation. *Palaeoapterodytes ictus* has the same data as *Palaeospheniscus intermedius*, but (again in my opinion) that species is not definable on available evidence. (As shown below, Ameghino's definition was based on an odd mistake.) The holotype of *Paraptenodytes antarcticus* was said by Ameghino to be from the "Patagónico medio" at the mouth of the Santa Cruz River. However, we found a specimen certainly of the same species in the basal Patagonia Formation opposite Gaiman (see Simpson, 1946). Thus there is at present no evidence that higher levels in the Patagonia Formation contain penguin species distinct from those at its base, although so few specimens are known from upper levels that the possibility of future discovery of some faunal difference is not excluded.

The Patagonia Formation contains enormous numbers of fossil invertebrates, and on the basis of those its age has come to be generally accepted as at least approximately early Miocene. The most extensive review and published original study is that by Feruglio (1949–1950), who confirmed that approximate dating. In spite of the large number of species involved, it is only approximate, and latest Oligocene age is not impossible. Some marine beds confused with or even included in parts of the Patagonia Formation may be older, but it remains highly probable that the greater or typical part of the formation is not older than late Oligocene, more likely early Miocene, and that the same determination applies to the fossil penguins.

Palaeospheniscus Moreno and Mercerat, 1891

Palaeospheniscus MORENO AND MERCERAT, 1891, p. 29. AMEGHINO, 1891, p. 440; 1895, p. 586; 1898, p. 230; 1905, p. 98. LAMBRECHT, 1933, p. 226. LOWE, 1939, p. 291 (erroneously attributed to Ameghino, 1894). SIMPSON, 1946, p. 26. BRODKORB, 1963, p. 236.

Parasphenisicus AMEGHINO, 1905, p. 115. LAMBRECHT, 1933, p. 228. SIMPSON, 1946, p. 29. BRODKORB, 1963, p. 238.

Perisphenisicus AMEGHINO, 1905, p. 117. LAMBRECHT, 1935, p. 229. SIMPSON, 1946, p. 31. BRODKORB, 1963, p. 237.

Pseudosphenisicus AMEGHINO, 1905, p. 123. LAMBRECHT, 1933, p. 230. SIMPSON, 1946, p. 30. BRODKORB, 1963, p. 239.

ETYMOLOGIES: *Palaeospheniscus*, Greek *palaios*, ancient, plus *Spheniscus*, name of a Recent penguin, i.e., an ancient penguin; *Parasphenisicus*, Greek *para*, beside, plus *Spheniscus*, a genus of Recent penguins, i.e., a penguin relative;[1] *Perisphenisicus*, Greek *peri*, near, plus *Spheniscus*, i.e., a penguin relative; *Pseudosphenisicus*, Greek *pseudo-*, false, plus *Spheniscus*, i.e., like but not identical with a Recent penguin.

TYPE-SPECIES: *Palaeospheniscus*, *P. patagonicus*, designated by Ameghino (1891, p. 447); *Parasphenisicus*, *Palaeospheniscus bergi* Moreno and Mercerat, by original designation (Ameghino, 1905, p. 115); *Perisphenisicus*, *P. wimani*, by monotypy; *Pseudosphenisicus*, *P. interplanus*, by original designation (Ameghino, 1905, p. 123).

INCLUDED SPECIES (as valid): *Palaeospheniscus patagonicus* Moreno and Mercerat, 1891; *Palaeospheniscus bergi* Moreno and Mercerat, 1891; *Palaeospheniscus gracilis* Ameghino, 1899; *Perisphenisicus wimani* Ameghino, 1905.

INCLUDED SPECIES (as subjective synonyms): *Palaeospheniscus menzbieri* Moreno and Mercerat, 1891; *Palaeospheniscus interruptus*, Ameghino, 1905; *Palaeospheniscus medianus* Ameghino, 1905; *Palaeospheniscus planus* Ameghino, 1905; *Palaeospheniscus rothi* Ameghino, 1905; *Palaeospheniscus intermedius* Ameghino, 1905; *Palaeospheniscus affinis* Ameghino, 1905; *Palaeospheniscus nereius* Ameghino, 1905; *Pseudosphenisicus interplanus* Ameghino, 1905; *Pseudosphenisicus concavus* Ameghino, 1905; *Treleudytes crassus* Ameghino, 1905.

KNOWN DISTRIBUTION: Patagonia Formation, Patagonian Stage, mainly in basal beds, late Oligocene or early Miocene, Chubut and Santa Cruz, Argentina. The holotype of *Palaeospheniscus gracilis* was recorded as from the highest part of the *Pyrotherium* zone, the Deseadan Stage in present

[1] Ameghino, who may have proposed as many generic names as anyone with the possible exception of Linnaeus, augmented the supply by free use of such Greek prepositional and other prefixes as *para-* and *peri-*. Generally no more precise meaning was intended than indication of a relationship. See Simpson (1962).

nomenclature, considerably older than the Patagonian, but it was almost certainly a surface find derived from the immediately overlying basal Patagonian (see below).

DIAGNOSIS: Humerus relatively stout, slightly curved, shaft narrower proximally, with rounded preaxial angulation; tricipital fossa of moderate size, strongly bipartite, medial fossette smaller, deep, relatively distal; proximal end of humerus not markedly expanded. Tarsometatarsus elongate relative to most Spheniscidae, ratio of length to proximal width about 2.2–2.4; external intermetatarsal foramen proximal, subcircular; internal intermetatarsal foramen minute or absent; metatarsal fusion strong.

DISCUSSION: Ameghino's diagnoses of the four putative genera whose names are here considered synonymous referred to many different characters for each, not homologous characters throughout, and included few stated distinctions. The internal metatarsal sulcus was mentioned for all, but in terms that indicated that all were essentially the same, i.e., that this sulcus was superficial or essentially absent. The external intermetatarsal foramen was mentioned for *Palaeospheniscus* and *Pseudospheniscus*, but for both was said simply to be larger than in *Spheniscus*. The internal metatarsal foramen was mentioned for *Palaeospheniscus* and *Paraspheniscus*, but for both was said to be very small or negligible. In fact all these characters are essentially identical in all four supposed genera, and no character named for the other three distinguished any of them from *Palaeospheniscus* as diagnosed by Ameghino.

Ameghino's diagnoses did differ for *Paraspheniscus* and *Perispheniscus* in that for the former a fossa at the upper (proximal) end of metatarsal II was said to be absent but in the latter subarcuate and deep. This difference exists in the holotypes of the type-species, which do belong to different species, but it seems to me a specific distinction, at most, and perhaps only individual. No stated character for *Pseudospheniscus* is a clear distinction from the diagnoses of any of the other genera, and I can see no such distinctive character. Ameghino's figure (1905, pl. 3, fig. 19a) makes it appear that *Pseudospheniscus* had a large internal intermetatarsal foramen, but that is not stated in the diagnosis and was merely restored by the artist in a manifestly impossible way.

In short, these four supposed genera have not been clearly distinguished, and on data now available I do not believe them to be adequately distinguishable.

Ameghino (1905) included 14 supposed species in the four supposed genera here united. All species would appear to be at least approximately synchronous and sympatric, their morphological differences are slight and

inconstant, the size range is not great, and therefore the recognition of so many species is almost obviously incorrect. Certainly no two holotypes are absolutely identical in every detail, but that is normally true of any species in nature and is demonstrably true of quite large collections of specimens of single Recent species. I have been unable to recognize associations of characters that seem to be reasonably constant and that could, together with size, be taken as distinctive of probably natural species.

The range in size, however, is definitely too great for a single species, demands that at least two be represented, and suggests that three or four are present. The 14 holotypes or lectotypes, all tarsometatarsi, and also some other skeletal elements, especially humeri, permit sorting into four size groups each of which seems to be comparable in variation with what might be expected in equally small samples from Recent species. The grouping by size is shown in table 1. I have tentatively called these size groups species, and I have applied to each the senior specific name represented by an included holotype. It is of course still quite possible that even four species are still too many, or that lines of separation between the groups may prove to be incorrectly drawn when and if really adequate samples become available. For example, *P. bergi* as here delimited might prove to be based on large variants of *P. gracilis*, small variants of *P. patagonicus*, or a mixture of the two. However, the present attempt is believed to be a reasonable, tentative conclusion from the data actually at hand.

Palaeospheniscus gracilis Ameghino, 1899

Palaeospheniscus gracilis AMEGHINO, 1899, p. 9. SIMPSON, 1946, p. 24, figs. 12A (humerus), 17D (carpometacarpus). BRODKORB, 1963, p. 236.

?Palaeospheniscus gracilis AMEGHINO, 1905, p. 111, pl. 2, fig. 9 (tarsometatarsus). LAMBRECHT, 1933, p. 228.

Palaeospheniscus nereius AMEGHINO, 1901, p. 81.

Paraspheniscus nereius: AMEGHINO, 1905, p. 116, pl. 2, fig. 13 (tarsometatarsus). LAMBRECHT, 1933, p. 229. SIMPSON, 1946, p. 30. BRODKORB, 1963, p. 238.

Palaeospheniscus medianus AMEGHINO, 1905, p. 108, pl. 1, fig. 6 (tarsometatarsus). LAMBRECHT, 1933, p. 227. SIMPSON, 1946, p. 26. BRODKORB, 1963, p. 236 (as synonym of *P. gracilis*).

ETYMOLOGIES: *P. gracilis*, Latin *gracilis*, slender, as the smallest species referred to the genus; *P. nereius*, Latin *nereius*, pertaining to Nereis, a sea nymph, daughter of the sea god Nereus, evidently from the marine habitus of the species; *P. medianus*, Latin *medianus*, middle, significance not stated by the author and not clear.

HOLOTYPES: *P. gracilis*, MACN (unnumbered), tarsometatarsus collected by Carlos Ameghino in the Patagonian of the Golfo de San Jorge; *P. medianus*, MLP (unnumbered), incomplete tarsometatarsus collected by

S. Roth in the Patagonian near Trelew.

HYPODIGM: The types, as above, and the following, all isolated bones from the basal Patagonian in the vicinity of Trelew and Gaiman in the valley of the Chubut River:

Humeri: AMNH 3288, 3313, 3345.
Radius: AMNH 3292.
Ulna: AMNH 3301.
Carpometacarpi: AMNH 3322, 3326, 3334.
Femur: AMNH 3279.
Tarsometatarsus: AMNH 3325.

TABLE 1

MEASUREMENTS OF TARSOMETATARSI AFTER AMEGHINO (1905) OF HIS HOLOTYPES OF SPECIES HERE REFERRED TO *Palaeospheniscus*

	Maximum Length	Proximal Width	Distal Width
Palaeospheniscus gracilis			
Holotype	32	14	—
Holotypes of synonyms			
P. nereius	32	14.5[a]	18
P. medianus	32	14	—
Palaeospheniscus bergi			
Holotype	35	15	21
Holotypes of synonyms			
P. planus	36	15.5[a]	19
P. rothi	35	15.5[a]	20
Pseudospheniscus interplanus[b]	—	—	—
Pseudospheniscus concavus[b]	—	—	—
Palaeospheniscus patagonicus			
Holotype	39	17.4	22
Holotypes of synonyms			
P. menzbieri	39	17	21.5[a]
P. interruptus	—	17	—
P. intermedius	39	16.5[a]	21.5[a]
P. affinis	38	15	21
Palaeospheniscus wimani			
Holotype	42.5[a]	18.5[a]	24

[a] It is evident that Ameghino was measuring to halves, not to tenths, of a millimeter.

[b] The measurements in question cannot be taken on these specimens, but they are close to the size of the three preceding.

These specimens are referred with some confidence, but the present concept of the species is based essentially on the humeri and tarsometatarsi.

KNOWN DISTRIBUTION: Most specimens are from the basal Patagonian of the Chubut River Valley near Trelew and Gaiman. Others may be from other levels and localities, although with the following exception there is no definite record of such. The holotype of *P. gracilis* was first recorded (Ameghino, 1899) as from the "Guaranítico de Patagonia." The name "Guaranitíco" was used by Ameghino for a large and miscellaneous group of rocks, not now considered to be a unit, believed by Ameghino to be coextensive with the Upper Cretaceous, but now believed to be mostly of early Tertiary age with some doubtful latest Cretaceous ("Rocan" and "Luisan") at the base. Later, Ameghino (1905) said more explicitly that the holotype was "coleccionado por C. Ameghino en la parte más superior del horizonte pyrotheriense, en el golfo de San Jorge." Ameghino's "horizonte pyrotheriense" is the stage now called Deseadan ("Deseadense" in Spanish) and generally considered more or less early Oligocene in age, although the correlation with the European Oligocene is quite insecure. "En el golfo de San Jorge" was of course not meant literally. That was a loose designation used for exposures not only anywhere along the shore of that large gulf but also for considerable distances inland. In this case the locality was certainly not the penguin-rich area around Trelew and Gaiman, because neither the Ameghinos nor anyone else has ever recognized any Deseadan (or "pyrotheriense") in that region. It was almost certainly the locality called "Rio Chico 1er yac. Pyroth." on the Ameghinos' labels (see Simpson, 1967, p. 65 and locality 8 on map, fig. 3), later commonly known as Cabeza Blanca (following Loomis, 1914). As Don Carlos informed me in 1931, he had been collecting there not long before Don Florentino's publication of 1899, and their knowledge of the "pyrotheriense" fauna at that time was largely based on fossils from that locality. (Unfortunately he did not explicitly include the penguin bone in his remarks.) At that locality richly fossiliferous basal Patagonian immediately overlies the uppermost Deseadan, and Patagonian fossils (mostly invertebrates) occur on the surface of the Deseadan. In 1931 at this locality I found a number of fossils, including at least one penguin bone, strewn down the exposure but evidently derived from the Patagonian capping of the hill. The holotype of *P. gracilis* cannot (in my opinion) be distinguished specifically from specimens certainly from the Patagonian in the Trelew-Gaiman area. The Deseadan, wherever known, is strictly nonmarine, but all the fossil penguins of definitely known origin throughout the world were in marine beds, and none has been surely established as from nonmarine beds. With all these considerations taken into account, it can be concluded that the

holotype of *P. gracilis*, like all other Patagonian fossil penguins yet known, is from the Patagonian Stage.

DIAGNOSIS: Smallest species now recognized in *Palaeospheniscus*. See measurements of tarsometatarsi in table 1.

DISCUSSION: Even though they were placed in two different genera by Ameghino, the holotypes of the three specific names here involved are so nearly identical in every preserved respect that there is little doubt that they are synonymous.

Palaeospheniscus bergi Moreno and Mercerat, 1891

Palaeospheniscus Bergi MORENO AND MERCERAT, 1891, p. 34, pl. 1, fig. 2 (humerus), fig. 4 (humerus), figs. 18–20 (radius), fig. 25 (corasoid), fig. 26 (metacarpus), pl. 2, fig. 7 (sternum), fig. 8 (tarsometatarsus). AMEGHINO, 1895, p. 587; 1898, p. 230. WIMAN, 1905b, p. 12.

Palaeospheniscus Bergii: AMEGHINO, 1891, p. 447.

Palaeospheniscus bergi: LOWE, 1933, p. 511.

Parasphenisicus Bergi: AMEGHINO, 1905, p. 115, pl. 2, fig. 12 (tarsometatarsus). LAMBRECHT, 1933, p. 228.

Parasphenisicus bergi: SIMPSON, 1946, p. 30. BRODKORB, 1963, p. 238.

Palaeospheniscus planus AMEGHINO, 1905, p. 109, pl. 1, fig. 7 (tarsometatarsus), pl. 2, fig. 7 (tarsometatarsus). LAMBRECHT, 1933, p. 227. SIMPSON, 1946, p. 27.

[?]*Palaeospheniscus planus:* BRODKORB, 1963, p. 327 (as synonym of *P. menzbieri*).

Palaeospheniscus Rothi AMEGHINO, 1905, p. 110, pl. 2, fig. 8 (tarsometatarsus). LAMBRECHT, 1933, p. 227.

Palaeospheniscus rothi: SIMPSON, 1946, p. 26. BRODKORB, 1963, p. 237.

Pseudospheniscus interplanus AMEGHINO, 1905, p. 123, pl. 3, fig. 19 (incomplete tarsometatarsus). LAMBRECHT, 1933, p. 230. SIMPSON, 1946, p. 30. BRODKORB, 1963, p. 240.

Pseudospheniscus planus AMEGHINO, 1905, p. 164 (an objective synonym of *P. interplanus;* BRODKORB, 1963, picked *interplanus* as first reviser, but this had in effect already been done by Lambrecht, 1933). BRODKORB, 1963, p. 240 (as rejected objective synonym of *P. interplanus*).

?*Pseudospheniscus concavus* AMEGHINO, 1905, p. 124, pl. 3, fig. 20 (tarsometatarsus). LAMBRECHT, 1933, p. 230.

Pseudospheniscus concavus: SIMPSON, 1964, p. 30. BRODKORB, 1963, p. 240.

Pseudospheniscus convexus AMEGHINO, 1905, p. 164 (an objective synonym of *P. concavus*; BRODKORB, 1963, picked *P. concavus* as first reviser, but this had in effect already been done by Lambrecht, 1933). BRODKORB, 1963, p. 24 (as rejected objective synonym of *P. concavus*).

ETYMOLOGIES: *P. bergi*, for Carlos Berg, a member of the staff of the Museo de La Plata under F. P. Moreno; *P. planus*, Latin *planus*, flat, presumably because the surface sculpture of the tarsometatarsus was said to be less salient than in *P. patagonicus; P. rothi*, for Santiago Roth, a Swiss naturalized in Argentina who collected in Patagonia and worked at the Museo de La Plata, originator of the concept and term Notoungulata; *P. interplanus*, I do not find a classical precedent for "interplanus" and

presume that it was an arbitrary coinage from Latin *inter*, between, and *planus*, flat, without obvious significance but perhaps to avoid confusion with *Palaeospheniscus planus*. The name *Pseudospheniscus planus*, used in Ameghino's plate legend for a figure of the holotype, may in fact have been meant, and *interplanus* in the text be the lapsus, because Ameghino (1905, p. 123) remarked on the "cara superior completamente plana" of metatarsal III. However, first Lambrecht and later Brodkorb selected *interplanus*, which prevents the name from being a homonym in *Palaeospheniscus*. *P. concavus*, Latin *concavus*, hollow or concave; the distal part of the plantar surface of the holotype tarsometatarsus is concave (as, indeed, is common at least as a variation in species of *Palaeospheniscus*). However the part proximal to that is said to be longitudinally convex. The name *convexus* was applied to the same specimen in the legend to a plate and it is not clear whether *concavus* or *convexus* was the lapsus, but first Lambrecht and later Brodkorb took the name *concavus*.

SYNTYPES OF *P. bergi*: MLP (unnumbered). Humerus, radius, metacarpus, femur, tarsometatarsus, sternum, and coracoid, probably not associated and not clearly all of the same species.

LECTOTYPE OF *P. bergi*: The tarsometatarsus in the syntype series, collected by L. J. Fontana in the Patagonia Formation near Trelew. Lectotype selected by Ameghino (1891, p. 587).

HOLOTYPES: *P. planus*, MACN (unnumbered), tarsometatarsus collected by C. Ameghino in the Patagonia Formation of the "Golfo de San Jorge"; *P. rothi*, MLP (unnumbered), tarsometatarsus collected by S. Roth in the Patagonia Formation near Trelew; *P. interplanus*, MACN (unnumbered), a tarsometatarsus collected by C. Ameghino in the lower Patagonia Formation near San Julián; *P. concavus*, MACN (unnumbered), a tarsometatarsus collected by C. Ameghino in the lower Patagonia Formation near San Julián.

HYPODIGM: For present purposes, the above listed lectotype and holotypes only. Other specimens, especially in the American Museum of Natural History and the British Museum (Natural History) probably belong to this species, but the reference is not certain enough for inclusion in the hypodigm.

KNOWN DISTRIBUTION: Patagonian Stage, Patagonia. Specimens of definitely recorded origin are from the lower Patagonia Formation in the regions of Trelew, Chubut, and San Julián, Santa Cruz.

DIAGNOSIS: Larger than *P. gracilis* and smaller than *P. patagonicus*. See measurements of tarsometatarsi in table 1.

DISCUSSION: It has been noted above that no character given by Ameghino for *Paraspheniscus* really distinguishes it from *Palaeospheniscus*, and once

Parasphenisscus bergi is placed in, or rather returned to, *Palaeosphenisscus* it cannot reasonably be separated from other specimens of the same size group in that genus referred to *P. planus* and *P. rothi*. The two supposed species placed by Ameghino in *Pseudosphenisscus* are radically incomplete in the same way. Both are distal ends, only, of metatarsals II and III. That gives them a spurious special resemblance to each other and a spurious apparent difference from more complete specimens of the same size.

Palaeosphenisscus patagonicus Moreno and Mercerat, 1891

Palaeosphenisscus patagonicus Moreno and Mercerat, 1891, p. 31, pl. 1, fig. 7 (femur), figs. 8–9 (humerus), fig. 12 (femur), fig. 13 (carpometacarpus), figs. 15-16 (tibiotarsus), fig. 21 (radius), fig. 25 (coracoid), fig. 27 (ulna), pl. 2, fig. 5 (tarsometatarsus). Ameghino, 1891, p. 447; 1895, p. 587; 1898, p. 230; 1905, p. 99, pl. 1, figs. 1–2 (tarsometatarsi). Wiman, 1905b, p. 12. Lambrecht, 1933, p. 226. Simpson, 1946, p. 28, fig. 11E (coracoid), fig. 12B (humerus), fig. 13C (humerus), fig. 14B (humerus), fig. 15C (radius), fig. 16C (ulna), fig. 17C (carpometacarpus), fig. 19D (restored wing bones), fig. 20A (femur), fig. 21C–D (tibiotarsus), fig. 22D (tarsometatarsus), fig. 23D (humerus), fig. 23I (tarsometatarsus). Brodkorb, 1963, p. 236.

Palaeosphenisscus Menzbieri Moreno and Mercerat, 1891, p. 33, pl. 1, fig. 1 (humerus), fig. 3 (humerus), fig. 5 (humerus), fig. 6 (humerus), fig. 10 (tibiotarsus), fig. 11 (tibiotarsus), fig. 14 (ulna), fig. 17 (carpometacarpus), fig. 22 (tibiotarsus), fig. 24 (coracoid), pl. 2, fig. 6 (tarsometatarsus). Ameghino, 1891, p. 447; 1895, p. 587; 1898, p. 230; 1905, p. 103, pl. 1, fig. 3 (tarsometatarsus). Lambrecht, 1933, p. 226.

Palaeosphenisscus menzbieri: Simpson, 1946, p. 27. Brodkorb, 1963, p. 237.

Palaeosphenisscus interruptus Ameghino, 1905, p. 104, pl. 1, fig. 4 (tarsometatarsus). Lambrecht, 1933, p. 227. Simpson, 1946, p. 28. Brodkorb, 1963, p. 237 (as synonym of *P. menzbieri*).

Palaeosphenisscus intermedius Ameghino, 1905, p. 113, pl. 2, fig. 10 (tarsometatarsus). Lambrecht, 1933, p. 227. Simpson, 1946, p. 27. Brodkorb, 1963, p. 237 (as synonym of *P. rothi*).

Palaeosphenisscus affinis Ameghino, 1905, p. 114, pl. 2, fig. 11 (tarsometatarsus). Lambrecht, 1933, p. 228. Simpson, 1946, p. 27. Brodkorb, 1963, p. 237 (as synonym of *P. rothi*).

Etymologies: *P. patagonicus*, Neolatin *patagonicus*, Patagonian; *P. menzbieri*, for M. Menzbier, a Russian ornithologist who wrote on (Recent) penguins; *P. interruptus*, Latin *interruptus*, broken, probably because the external intermetatarsal sulcus is said to be interrupted, although this does not seem to be a clear distinction from other forms of the genus; *P. intermedius*, Latin *intermedius*, in the middle or between two, probably because Ameghino considered it transitional in some respects from *Palaeosphenisscus* to *Parasphenisscus; P. affinis*, Latin *affinis*, neighboring, related, probably because Ameghino recognized its close relationship (I believe specific identity) with *P. intermedius*.

SYNTYPES OF *P. patagonicus:* MLP (unnumbered) humerus, radius, ulna, carpometacarpus, femur, tibiotarsus, tarsometatarsus, coracoid, scapula, and vertebrae not associated and not assuredly all of the same species.

LECTOTYPE: The tarsometatarsus among the syntypes, collected by L. J. Fontana in the Patagonian near Trelew. Selected by Ameghino (1891, p. 447).

SYNTYPES OF *P. menzbieri:* MLP (unnumbered) coracoid, humerus, ulna, radius, carpometacarpus, tarsometatarsus, vertebrae, and sternum not associated and not assuredly all of the same species.

LECTOTYPE: The tarsometatarsus among the syntypes, collected by L. J. Fontana in the Patagonian near Trelew. Selected by Ameghino (1891, p. 447).

HOLOTYPES: *P. interruptus*, MLP (unnumbered) incomplete tarsometatarsus collected by S. Roth in the Patagonian near Trelew; *P. intermedius*, MACN (unnumbered) tarsometatarsus collected by C. Ameghino in the upper Patagonia Formation of the "Golfo de San Jorge"; *P. affinis*, MLP (unnumbered) tarsometatarsus collected by S. Roth in the Patagonian near Trelew.

HYPODIGM: The lectotypes and holotypes as above and also the following, all isolated bones from the basal Patagonian near Trelew and Gaiman:

Humeri: AMNH 3285, 3287, 3289, 3340, 3343, 3344, 3352.

Radius: AMNH 3298.

Ulnae: AMNH 3295–3297.

Carpometacarpi: AMNH 3316, 3323, 3336.

Femora: AMNH 3274, 3276, 3349, 3355.

Tibiotarsi: AMNH 3321, 3330.

Tarsometarsus: AMNH 3358.

There are numerous other specimens probably of this species in the collections, but at present only the above are included in the hypodigm, and only the humeri and tarsometatarsi are used in specific definition.

KNOWN DISTRIBUTION: Patagonia Formation of Patagonia. One specimen is recorded as from the upper Patagonia, but its locality is unknown. Other specimens of known level are from the basal Patagonia, and all specimens of known locality are from near Trelew and Gaiman.

DIAGNOSIS: Larger than *P. bergi* and smaller than *P. wimani*. See measurements of tarsometatarsi in table 1.

DISCUSSION: The holotypes of *P. patagonicus*, *menzbieri*, *interruptus*, and *intermedius* seem quite obviously within the probable range of a single species. Although Ameghino's descriptions are verbally different, they simply refer in part to different characters, in part to normal individual variation, and in part to differences of preservation. At first sight the

holotype of *P. affinis* looks more distinctive, especially in its relatively narrow proximal end, but I believe this caused by imperfect preservation of that part of the bone.

Palaeospheniscus wimani (Ameghino, 1905)

Perispheniscus Wimani AMEGHINO, 1905, p. 117, pl. 2, fig. 14 (tarsometatarsus), pl. 3, fig. 14 (tarsometatarsus), fig. 15 (humerus). LAMBRECHT, 1933, p. 229, fig. 94A (tarsometatarsus, after Ameghino).

Perispheniscus wimani: SIMPSON, 1946, p. 32. BRODKORB, 1963, p. 238 (as synonym of "*Perispheniscus*" *robustus*).

Palaeospheniscus robustus: SIMPSON, 1946, p. 28 (in error; the holotype of *Palaeospheniscus robustus* belongs in *Paraptenodytes*, see below; most or all the specimens called *Palaeospheniscus robustus* and of the following figures so named in Simpson, 1946, belong to *Palaeospheniscus wimani*), fig. 12E (humerus), fig. 15B (radius), fig. 16B (ulna), fig. 17B (carpometacarpus), fig. 19C (restoration of wing bones); 1970, p. 19 seq., pl. 3, figs. 2–3 (also specimens of *P. wimani* erroneously labeled *P. robustus*).

ETYMOLOGY: For C. Wiman, Swedish paleontologist, who first described fossil penguins from Seymour Island.

TYPE OF *P. wimani:* MLP (unnumbered), tarsometatarsus from the Patagonia Formation of the Patagonian coast. Collector and locality not recorded.

HYPODIGM: The holotype and the following, all isolated bones from near the base of the Patagonia Formation in the region of Trelew and Gaiman:

Humerus: AMNH 3361.

Radius: AMNH 3350.

Ulnae: AMNH 3300, 3303, 3360.

Carpometacarpus: AMNH 3337.

Femur: AMNH 3277.

Tibiotarsi: AMNH 3328, 3348.

Tarsometatarsus: AMNH 3324.

Although those specimens are believed to belong to this species, and a number of others in the various collections may do so, the present specific concept is based mainly on the humerus and the tarsometatarsi.

KNOWN DISTRIBUTION: Patagonia Formation of Patagonia. Specimens of more exactly known origin are from near the base of the formation in the region of Trelew and Gaiman.

DIAGNOSIS: The largest species now recognized in *Palaeospheniscus*. See measurements of tarsometatarsi in table 1.

DISCUSSION: This is the species that has generally but erroneously been called "*Palaeospheniscus robustus*" in the literature after 1895; see discussion of *Paraptenodytes robustus*, below. Although represented by only one of Ameghino's types, it is rather abundant, as shown by the AMNH collection,

and is readily recognized as a size group. Reference to *Palaeospheniscus* is supported by humeri similar to *Palaeospheniscus* except in size and distinct from *Chubutodyptes* or *Paraptenodytes*.

CHUBUTODYPTES SIMPSON, 1970

Chubutodyptes SIMPSON, 1970, p. 21.

ETYMOLOGY: Chubut, the territory where the specimens were found, and Greek *dyptes*, diver.

TYPE-SPECIES: *C. biloculata*.

KNOWN DISTRIBUTION: Lower Patagonia Formation, Chubut, Argentina.

DIAGNOSIS: Humerus generally similar to that of *Palaeospheniscus* but with proximal end widely expanded lateromedially, bicipital fossa large but relatively shallow, bipartite with the two parts subequal in size and depth and almost directly medial and lateral with respect to each other.

DISCUSSION: In 1946 (Simpson, 1946, p. 51) I mentioned the presence in the American Museum collection of two partial humeri evidently of an unnamed species and possibly an unnamed genus related to *Palaeospheniscus*, and one was figured (Simpson, 1946, fig. 13B). No name was given at that time because of the incompleteness of the specimens. However, no better specimens have appeared, these are fully characteristic, and in connection with later restudy I therefore named the genus and species.

The humerus is larger than any currently referred to *Palaeospheniscus*, and the bicipital fossa is distinctly different, as noted in the diagnosis. It is of special interest because no other early to middle Tertiary penguin this large or larger so far known has a bipartite bicipital fossa.

Chubutodyptes biloculata Simpson, 1970

Chubutodyptes biloculata SIMPSON, 1970, p. 22, pl. 4, figs. 1–4 (humeri).

ETYMOLOGY: Latin *biloculata*, two-chambered, in reference to the tricipital fossa.

HOLOTYPE: AMNH 3346, imperfect proximal and medial parts of humerus, collected by me in the basal Patagonia Formation at Cerro Castillo near Trelew.

HYPODIGM: The holotype and AMNH 3341, somewhat broken proximal half of a humerus, collected by me in the basal Patagonia Formation opposite (south of) Gaiman.

KNOWN DISTRIBUTION: Basal Patagonia, Chubut.

DIAGNOSIS: Only known species of the genus as diagnosed above.

REMARKS: The specimen AMNH 3361 used for comparison with this species and figured in the same publication (Simpson, 1946. pl. 3, figs. 2-3)

was then referred to "*Palaeospheniscus robustus*," but is now referred to *Palaeospheniscus wimani*.

PARAPTENODYTES AMEGHINO, 1891

Paraptenodytes AMEGHINO, 1891, p. 447; 1895, p. 589; 1898, p. 230; 1905, p. 138. LAMBRECHT, 1933, p. 232. SIMPSON, 1946, p. 33. BRODKORB, 1963, p. 238.

Metancylornis AMEGHINO, 1905, p. 129. LAMBRECHT, 1933, p. 231. SIMPSON, 1946, p. 32. BRODKORB, 1963, p. 238 (as synonym of *Paraptenodytes*).

Isotremornis AMEGHINO, 1905, p. 134. LAMBRECHT, 1933, p. 232. SIMPSON, 1946, p. 33. BRODKORB, 1963, p. 239.

Treleudytes AMEGHINO, 1905, p. 156. LAMBRECHT, 1933, p. 235. SIMPSON, 1946, p. 31. BRODKORB, 1963, p. 237 (as synonym of *Perispheniscus*).

ETYMOLOGIES: *Paraptenodytes*, Greek *para*, beside, plus *Aptenodytes*, a genus of Recent penguins, i.e. a penguin relative; *Metancylornis*, Greek *meta-*, following, after, *ancylos*, curved, *ornis*, bird. The significance is not clear to me; perhaps *Ancylornis* designates another bird with which this one was compared, but the name is not known to me and the only explicit comparison by Ameghino was with *Pygoscelis*, a well-known genus of Recent penguins. *Isotremornis*, Greek *iso-*, equal, *trema*, hole, and *ornis*, bird, because the two intermetatarsal foramina in the tarsometatarsus are approximately equal; *Treleudytes*, Trelew, the town near which the holotype of the type-species was found, and Greek *dytes*, diver, a word used in a number of names of penguin genera.

TYPE-SPECIES: *Paraptenodytes: Palaeospheniscus antarcticus*, by monotypy and author's designation; *Metancylornis*, *Paraptenodytes curtus*, by monotypy and author's designation; *Isotremornis*, *I. Nordenskjöldi*, by monotypy and author's designation; *Treleudytes*, *T. crassus*, by monotypy.

SPECIES INCLUDED (as valid): *Paraptenodytes antarcticus*, *Palaeospheniscus robustus*, *Paraptenodytes brodkorbi*.

SPECIES INCLUDED (as probable subjective synonyms): *Isotremornis Nordenskjöldi* (original, now invalid, spelling), *Metancylornis curtus*, and dubiously *Treleudytes crassus*.

KNOWN DISTRIBUTION: Patagonia Formation, Patagonian Stage, mainly or entirely from lower part, Chubut and Santa Cruz, Argentina.

DIAGNOSIS: Humerus moderately elongate, nearly st raight,shaft slightly narrower proximally; preaxial angle slight, distal, rounded; tricipital fossa deep, not bipartite. Tarsometatarsus short and stout, ratio of length to proximal width approximately 2 or less; metatarsals strongly fused but with two, small, proximal intermetatarsal foramina, subequal in type-species but lateral foramen larger is referred species.

DISCUSSION: Because of the discovery of extensive parts of associated skull and skeleton of the type-species, fully described elsewhere (Simpson,

1946), this is the best-known genus of fossil penguins. The most widely diagnostic parts,[1] humerus and tarsometatarsus, are fully distinctive. Ameghino (1905) mentioned the resemblance of his *Isotremornis nordenskjoeldi* to *Metancylornis* but did not compare it with *Paraptenodytes antarcticus*, from which I believe it should not be distinguished specifically. *Metancylornis* was based on a species, *curtus*, originally referred to *Paraptenodytes*. The only noteworthy distinction given was that the internal intermetatarsal foramen is notably smaller than the external. I believe that the size of the latter in the holotype is exaggerated by abrasion or breakage, and in any case would not consider the difference more than specific. The specimens under comparison are specifically distinct. The holotype of the type-species of *Treleudytes* has the basic characters of *Paraptenodytes* but is more elongate than other specimens of tarsometatarsi so far referred to that genus and to that extent is closer to *Palaeospheniscus*. The position of *Treleudytes crassus* is still somewhat uncertain and is discussed under the species.

Paraptenodytes antarcticus (Moreno and Mercerat, 1891)

Palaeospheniscus antarcticus Moreno and Mercerat, 1891, p. 30, pl. 2, fig. 1 (femur), fig. 2 (tibiotarsus), fig. 4 (tarsometatarsus). Wiman, 1905b, p. 12.

Paraptenodytes antarcticus: Ameghino, 1891, p. 447; 1895, p. 589, fig. 37 (mandible); 1898, p. 230, fig. 91, VIII (mandible); 1905, p. 139, fig. 2 (mandible), pl. 5, fig. 32 (tarsometatarsus), pl. 6, fig. 33 (femur), fig. 34 (tibiotarsus). Lambrecht, 1933, p. 232. Simpson, 1946, p. 33, fig. 1 (skull), fig. 2 (articular), fig. 3 (scapula), fig. 4 (coracoid), fig. 5 (humerus), fig. 6 (femur), fig. 7 (tibiotarsus), fig. 8 (tarsometatarsus), fig. 11B (coracoid), fig. 12H (humerus), fig. 14A (humerus), fig. 21A, B (tibiotarsus), fig. 22A, G (tarsometatarsus), fig. 23C (humerus), fig. 23H (tarsometatarsus), fig. 26C (skull), fig. 27A (pterygoid), fig. 28A (quadrate), fig. 30B (humerus). Brodkorb, 1963, p. 238.

Isotremornis Nordenskjöldi Ameghino, 1905, p. 134, pl. 4, fig. 28 (tarsometatarsus),[2] pl. 5, figs. 29–30 (humerus), fig. 31 (femur). Lambrecht, 1933, p. 232.

Isotremornis nordenskjöldi: Simpson, 1946, p. 33.

Isotremornis nordenskjoeldi: Brodkorb, 1963, p. 239.

Etymologies: *P. antarcticus*, Neolatin *antarcticus*, Antarctic, an inappropriate name as the known distribution is far from the Antarctic by any definition; *I. Nordenskjöldi*, for Otto Nordenskjöld, Swedish explorer,

[1] Skulls are most diagnostic for Recent penguins, but partial skulls are known for only two quite different fossil penguins and they are not a practical means of diagnosis or identification for fossils in this group.

[2] Two figures on this plate are marked 28a. The one on the upper right is "*I. Nordenskjöldi*." The one on the lower right is "*Eospheniscus Gunnari*" and should have been marked 27a.

whose party made the discovery of fossil penguins on Seymour Island. As noted by Brodkorb, the latest version of the International Code of Zoological Nomenclature requires the spelling *nordenskjoeldi*.

SYNTYPES OF *P. antarcticus*: MLP (unnumbered), supposedly associated femur, tibiotarsus, tarsometatarsus, and dissociated ulna, femur, and tibia.

LECTOSYNTYPES OF *P. antarcticus*: Although he did not formally so state, Ameghino in effect made a lectotype selection when he listed as type only the femur, tibiotarsus, and tarsometatarsus which he believed to belong to one individual. They were found by C. Ameghino in the middle Patagonian at the mouth of the Santa Cruz River.

LECTOTYPE OF *P. antarcticus*: The tarsometatarsus, only, of the original syntypes is hereby designated as sole lectotype. Although the three bones designated by Ameghino may be of one individual, this is not demonstrable, and for absolute security a single specimen should be taken as lectotype.

HOLOTYPE OF *I. nordenskjoeldi*: MACN (unnumbered), proximal part of a tarsometatarsus, collected by C. Ameghino in the lower Patagonia Formation of San Julián. Ameghino (*loc. cit.*) stated that this specimen was the type, accompanied by an almost complete humerus and parts of another humerus and of a femur, apparently of the same individual. I (Simpson, 1946) took it that Ameghino considered all these bones as parts of his type and therefore, whether correctly associated or not, as syntypes. The first-mentioned bone, the tarsometatarsus, is specifically inseparable from *Paraptenodytes antarcticus* but the more complete humerus definitely does not belong to that species. In order to conserve Ameghino's name and intention, I therefore designated the humerus as lectotype (Simpson, 1946, p. 33). However, Brodkorb (1963, p. 239) concluded that Ameghino's wording made the tarsometatarsus the holotype even though Ameghino also listed the other bones as "associated," and Brodkorb therefore maintained that my designation of a lectotype was invalid. I now reluctantly accept that view, because it has a basis in the ambiguity of the original publication, and nomenclature may be more readily stabilized in this way. Unfortunately, this makes *Isotremornis* a subjective (but nearly certain) synonym of *Paraptenodytes* and *I. nordenskjoeldi* similarly a subjective synonym of *P. antarcticus*. As the humerus that I would like to have made lectotype does not belong to that or any other named species once it is removed from *I. nordenskjoeldi*, it must unfortunately have a new name, which is proposed below.

HYPODIGM: The lectotype and holotype listed above and AMNH 3338, much of an associated skeleton as described in Simpson (1946). Other specimens in the various collections almost surely belong to this species,

TABLE 2

SOME MEASUREMENTS OF SPECIMENS REFERRED TO *Paraptenodytes* and *Arthrodytes*

	Tarsometatarsi			
	A. Total Length	B. Proximal Width	C. Distal Width	A/B
Paraptenodytes antarcticus				
Holotype	53	28	35	1.89
Holotype of synonym				
Isotremornis nordenskjoeldi	—	28	—	—
Paraptenodytes robustus				
Holotypes of synonyms				
Paraptenodytes curtus	42	24	—	1.75
Treleudytes crassus	41.5	20	24	2.07

	Humerus	
	Total length	Median width of shaft
Paraptenodytes antarcticus		
AMNH 3338	114.1	19.7
Paraptenodytes robustus		
Holotype	91.4	19.5
?*Paraptenodytes brodkorbi*		
Holotype	*ca.*98	*ca.*23
Arthrodytes grandis		
Lectotype of synonym		
A. andrewsi	149	29 (35 at the angle)

but the present concept of it is based on these.

KNOWN DISTRIBUTION: Patagonia Formation, Santa Cruz and Chubut, Argentina.

DIAGNOSIS: Largest species now recognized in the genus, see measurements in table 2. Shaft of humerus relatively long and slender, preaxial angle inconspicuous; tricipital fossa small, with narrow mouth, but deep. Intermetatarsal foramina subequal.

DISCUSSION: The partial humeri that Ameghino ascribed to *Isotremornis nordenskjoeldi* and believed to be part of the same individual as the present lectotype (Ameghino, 1905, p. 134 and pl. 5, figs. 29-30) almost certainly were not associated with the lectotype tarsometatarsus and do not belong to the present species. The lectotype of *I. nordenskjoeldi* is specifically indistinguishable from the lectotype of *P. antarcticus*. The humerus is well known in the latter species and is quite different from those placed in *I. norden-*

skjoeldi by Ameghino: larger and morphologically distinct. They are necessarily placed in new species, ?*P. brodkorbi*, described below.

Paraptenodytes robustus (Ameghino, 1895)

Palaeospheniscus robustus AMEGHINO, 1895, p. 588, fig. 36 (humerus); 1898, p. 230, fig. 91, VII (humerus); 1905, p. 105, fig. 1 (humerus), pl. 1, fig. 5 (tarsometatarsus; not in fact this species but *Palaeospheniscus wimani*). SAEZ, 1927, p. 77. LAMBRECHT, 1933, p. 227. SIMPSON, 1946, p. 28 (numerous other references to this species and figures so labeled are probably all *P. wimani*).

Perispheniscus robustus: BRODKORB, 1963, p. 237 (from the stated synonymy, there mistaken for *Palaeospheniscus wimani*).

Paraptenodytes curtus AMEGHINO, 1901, p. 81. BRODKORB, 1963, p. 239.

Metancylornis curtus: AMEGHINO, 1905, p. 129, pl. 4, fig. 25 (tarsometatarsus), fig. 26 (humerus). LAMBRECHT, 1933, p. 231. SIMPSON, 1946, p. 32.

Treleudytes crassa AMEGHINO, 1905, p. 156, fig. 4 (tarsometatarsus). LAMBRECHT, 1933, p. 235. BRODKORB, 1963, p. 238 (as synonym of *Palaeospheniscus robustus*).

Treleudytes crassus: SIMPSON, 1946, p. 31.

ETYMOLOGIES: *P. robustus*, Latin *robustus*, robust, at the time of description the largest species referred to *Palaeospheniscus*; *P. curtus*, Latin *curtus*, cut short, probably because the tarsometatarsus is shorter than that of *P. antarcticus; Treleudytes crassus*, Latin *crassus*, dense, solid, evidently taken in the sense of robust, as the holotype was said to be similar to *Perispheniscus* but "más robusto." Greek *dytes* is masculine and the name *Treleudytes* must be construed as of that gender. Under the Code, the original spelling *crassa* must therefore be amended to *crassus*.

SYNTYPES OF *P. robustus*: BM (NH) A/591, humerus and fragments of two dissociated femora. Patagonia Formation, La Cueva, Patagonia. (Brodkorb, 1963, stated incorrectly that the type was from Trelew.)

LECTOTYPE OF *P. robustus:* The humerus. Ameghino tacitly but not explicitly made this selection when he mentioned the humerus, only, as type in 1905 (p. 105). In case of any doubt, I hereby so designate.

SYNTYPES OF *P. curtus:* MACN (unnumbered) tarsometatarsus and dissociated fragment of humerus collected by C. Ameghino in the lower Patagonia Formation of San Julián.

LECTOTYPE OF *P. curtus*: The tarsometatarsus syntype, hereby selected. The fragment of a humerus included by Ameghino in the type is believed not to belong to the same species.

HOLOTYPE OF *T. crassus*: MACN (unnumbered), tarsometatarsus, collected by S. Roth in the Patagonia Formation of Trelew.

HYPODIGM: Although other specimens of this species probably occur in collections, the present conception of the species is based primarily on its lectotype, with the somewhat doubtful addition of the other lectotype and holotype listed above.

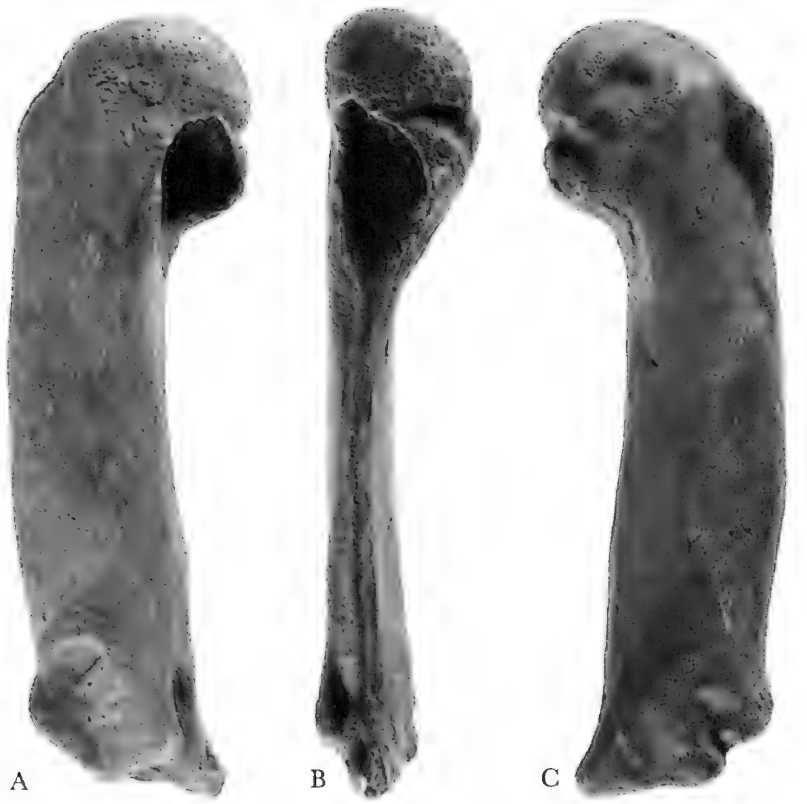

FIG. 1. *Paraptenodytes robustus* (Ameghino). Holotype, BM(NH) A/591, left humerus. A. Ventral view. B. Postaxial view. C. Dorsal view. All ×1.

KNOWN DISTRIBUTION: Patagonia Formation, Patagonia.

DIAGNOSIS: Smallest species now recognized in this genus, see measurements in table 2. Humerus broader in proportion to length than in *P. antarcticus*, but less so than in ?*P. brodkorbi;* tricipital fossa large and widely open; preaxial angulation virtually absent. Somewhat doubtfully referred tarsometatarsi similar to *P. antarcticus* but smaller and with external intermetatarsal foramen slightly or definitely larger than internal.

DISCUSSION: In March, 1896, shortly after publishing "*Palaeospheniscus*" *robustus*, Ameghino included the syntypes in a collection of fossil bird bones that he sold to the British Museum (Natural History). The catalogue entry there is as follows:

"Palaeospheniscus robustus. Am. Complete humerus. figd. loc. cit. fig. 36. The type. Also portions of two femora, not associated? Patagonian formation. La Cueva, Patagonia."

Ameghino's figure (1895, fig. 36, and later twice copied unchanged)

was not entirely accurate and also did not reveal that the tricipital fossa is not bipartite, a fact that in itself excludes reference to *Palaeospheniscus*. All other Patagonian penguin types are in Argentina, and no one reexamined this one until I did so in 1970. In the meantime everyone concerned, starting with Ameghino himself, assumed that *P. robustus* did indeed belong to *Palaeospheniscus* and referred to that species numerous specimens of *Palaeospheniscus* of approximately the same size, large for that genus. For a start, Ameghino (1905, p. 106 and pl. 1, fig. 5) referred to "*P.*" *robustus* a tarsometatarsus that does in fact belong to *Palaeospheniscus* and therefore cannot really belong to that species. As noted above, the name *P. wimani* is applicable to the large size group of true *Palaeospheniscus* hitherto incorrectly called *P. robustus*.

Although the lectotype of "*P.*" *robustus* is too small to belong to *Paraptenodytes antarcticus* and has somewhat different proportions, it has all the characters considered generic for *Paraptenodytes* and can conveniently be referred to that genus. The tarsometatarsus of *Paraptenodytes curtus*, although later made the basis for a separate genus *Metancylornis*, also has the generic characters of *Paraptenodytes* but is smaller than, and otherwise slightly different from, *P. antarcticus*. Its size is just what would be expected in a bird with a humerus the size of *P. robustus*, and it is a reasonable hypothesis, at least, that "*Metancylornis curtus*" is in fact based on the tarsometatarsus of *Paraptenodytes robustus*.

What to do with *Treleudytes crassus* remains more doubtful if not a wholly open question. The holotype tarsometatarsus, sole specimen placed in this supposed genus and species, is of about the same size as that of *Paraptenodytes curtus*, now referred to *P. robustus*. "*T. crassus*" also has a general resemblance to *Paraptenodytes*, but its tarsometatarsus is more elongate than others referred to that genus and also has the internal intermetatarsal foramen more reduced, almost vestigial. Those are resemblances to *Palaeospheniscus*, and "*T. crassus*" is also close to *P. wimani* in size. However, in other respects it is more like *Paraptenodytes*, and its tarsometatarsus is distinctly stouter than any confidently referred to *Palaeospheniscus*. I have here very tentatively considered "*T. crassus*" as a possible extreme variant of *Paraptenodytes robustus*, but it could be a likewise extreme variant of *Palaeospheniscus wimani* or, indeed, a valid separate species as Ameghino thought.

Paraptenodytes brodkorbi, new species

ETYMOLOGY: For Pierce Brodkorb whose decision as to the type of "*Isotremornis nordenskjoeldi*" made erection of this new species necessary.

HOLOTYPE: Humerus collected by C. Ameghino in the lower Patagonia

Formation of San Julián, figured by Ameghino (1905, pl. 5, fig. 29).

HYPODIGM: The holotype.

KNOWN DISTRIBUTION: As above in the Patagonia Formation for the only surely identified specimen.

DIAGNOSIS: Intermediate between *P. antarcticus* and *P. robustus* in size, see measurements in table 2. Humerus distinctly stouter than in those species and with a more sharply defined preaxial angle.

DISCUSSION: Although there is already a marked superfluity of specific names for this fauna, I do not see how any of them can be applied to this distinctive humerus. The humerus is known and is quite different in *Paraptenodytes antarcticus*, *P. robustus*, and *Palaeospheniscus wimani*. It is not known in the possibly valid species "*Treleudytes crassus*" unless that is, as seems probable, a synonym of one of the previously mentioned names, but the humerus of ?*P. brodkorbi* is probably too large to belong to the same species as the tarsometatarsus of "*T. crassus*."

ARTHRODYTES AMEGHINO, 1905

Arthrodytes AMEGHINO, 1905, p. 143. LAMBRECHT, 1933, p. 233. SIMPSON, 1946, p. 34. BRODKORB, 1963, p. 235.

ETYMOLOGY: Greek *arthron*, joint, *dytes*, diver, perhaps because the genus was essentially based on characters of the distal articulation of the femur.

TYPE-SPECIES: *Paraptenodytes grandis*, by author's designation.

SPECIES INCLUDED (as a subjective synonym): *Paraptenodytes andrewsi*.

KNOWN DISTRIBUTION: Patagonia Formation, Patagonia. The known specimens are from San Julián, Santa Cruz.

DIAGNOSIS: (Based on the lectotype of *Paraptenodytes andrewsi*.) Humerus less massive than in *Anthropornis* but more than in *Paraptenodytes*. Head deep dorsoventrally. Shaft above preaxial angle nearly straight, slightly tapering proximally, offset postaxially distal to the prominent preaxial angle. Tricipital fossa deep, moderate in comparison to size of the whole bone, not bipartite.

DISCUSSION: The original definition of this genus referred entirely to the distal end of the femur, lectotype of the type-species. This is one of the least characteristic parts of the penguin skeleton, and no other fossil genus or species has been based on it. On those grounds alone, the genus would be essentially indeterminate. However, as explained in discussion of the species, there are reasonable grounds to assume, or to postulate, that the lectotype humerus of "*Paraptenodytes andrewsi*" belongs to *Arthrodytes grandis*, and on that basis the genus is valid and can be clearly defined.

Ameghino (1905) suggested that his *Arthrodytes* might be a synonym of

Anthropornis Wiman from Seymour Island, and even that *Arthrodytes andrewsi* might be a synonym of *Anthropornis nordenskjoeldi*. Lambrecht (1933) and Simpson (1946) found that the separation of *Arthrodytes grandis* from *Anthropornis* was not clear, but that *Arthrodytes andrewsi* does not belong to that genus. Restudy, including that of Wiman's specimens and of others in the British Museum (Natural History), confirms that view. The humerus of *Arthrodytes andrewsi* (here equated with *A. grandis*) differs greatly from that of *Anthropornis*, notably in being much less massive, having a less sigmoid shaft, and a strongly projecting preaxial angulation. Brodkorb (1963) returned *andrewsi* to *Paraptenodytes*, but its humerus is also well distinguished from that of the type-species *Paraptenodytes antarcticus*, especially in being more massive, having a deeper (dorsoventrally) head, in having a sharp preaxial angulation, and in being offset below that angulation.

Arthrodytes grandis (Ameghino, 1901)

Paraptenodytes grandis AMEGHINO, 1901, p. 18.
Arthrodytes grandis: AMEGHINO, 1905, p. 144, pl. 5, fig. 35 (humerus), pl. 6, fig. 36 (femur). LAMBRECHT, 1933, p. 233. SIMPSON, 1946, p. 34. BRODKORB, 1963, p. 235.
Paraptenodytes Andrewsi AMEGHINO, 1901, p. 81.
Paraptenodytes andrewsi: BRODKORB, 1963, p. 239.
Arthrodytes Andrewsi: AMEGHINO, 1905, p. 146, pl. 7, fig. 37 (humerus), pl. 8, fig. 38 (coracoid), fig. 39 (scapula). LAMBRECHT, 1933, p. 233.
Arthrodytes andrewsi: SIMPSON, 1946, p. 35.

ETYMOLOGIES: *A. grandis*, Latin *grandis*, large, the largest fossil penguin known from Patagonia; *A. andrewsi*, for the English vertebrate paleontologist C. W. Andrews who, however, had no connection with penguins.

SYNTYPES OF *A. grandis*: MACN (unnumbered) distal end of femur and proximal end of humerus, collected by C. Ameghino in the lower Patagonia Formation of San Julián. Considered by F. Ameghino as surely of the same individual, but probably not so.

LECTOTYPE OF *A. grandis*: The partial femur, selected by Simpson (1946, p. 34).

SYNTYPES OF *A. andrewsi*: MACN (unnumbered), humerus, coracoid, and part of scapula, collected by C. Ameghino in the lower Patagonia Formation of San Julián. Considered by F. Ameghino as of the same individual, but possibly not so.

LECTOTYPE OF *A. andrewsi*: The humerus, selected hereby.

HYPODIGM: The two lectotypes.

KNOWN DISTRIBUTION: Lower Patagonia Formation, Santa Cruz. The known specimens are from San Julián.

DIAGNOSIS: Only species currently recognized in the genus as defined above.

DISCUSSION: Ameghino (1905) believed that the syntypes were surely from the same individual, but that is almost certainly wrong. On the basis of proportions in other penguins, the humerus head belonged to a significantly smaller species than the distal end of the femur. Because the generic and specific diagnoses were based on the femur, I (Simpson, 1946) made that lectotype. The other syntype, the head of a humerus, agrees almost precisely in both size and structure with the specimen here made holotype of ?*Paraptenodytes brodkorbi*, and I think it probably belongs to that species.

The lectotype of *A. andrewsi* is notably larger than the syntype humerus here removed from *A. grandis* and is, in fact, just the size that would be expected in a penguin with a femur of the size of the lectotype of *A. grandis*. It is a reasonable hypothesis, at least, that the complete humerus lectotype of *A. andrewsi* does belong to *A. grandis*.

SUPPOSED TAXA OF SPHENISCIDAE OF DOUBTFUL STATUS

NECULUS AMEGHINO, 1905

Neculus AMEGHINO, 1905, p. 127. LAMBRECHT, 1933, p. 231. SIMPSON, 1946, p. 26. BRODKORB, 1963, p. 240.

ETYMOLOGY: Araucanian Indian *neculú*, runner (derivation given exceptionally by Ameghino, 1905, p. 127, footnote).

TYPE-SPECIES: *N. rothi*, by monotypy.

KNOWN DISTRIBUTION: Geological data not given, but probably Patagonia Formation, the one known specimen from near Trelew.

ORIGINAL DIAGNOSIS: Translated from Spanish, "Tarsometatarsus very compressed anteroposteriorly, with the metatarsals in the same plane dorsally, the two intermetatarsal sulci deep, trochleae very small and a large impression on the internal side for the metatarsal of digit I."

DISCUSSION: The very poorly preserved bone fragment on which this genus was based probably belonged to a penguin, and perhaps to one smaller than other known fossils from Patagonia, but its true character is so dubious that its zoological value is little or nil at present.

Neculus rothi Ameghino, 1905

Neculus Rothi AMEGHINO, 1905, p. 127, pl. 4, fig. 23 (fragment of tarsometatarsus). LAMBRECHT, 1933, p. 231.

Neculus rothi: SIMPSON, 1946, p. 26. BRODKORB, 1963, p. 240.

ETYMOLOGY: For Santiago Roth, see etymology of *Palaeospheniscus rothi* in the synonymy of *P. bergi*.

HOLOTYPE: MLP (unnumbered), distomedial fragment of tarsometatarsus, collected by S. Roth near Trelew.

HYPODIGM: Holotype only.

KNOWN DISTRIBUTION: Probably Patagonia Formation, near Trelew, Chubut.

DIAGNOSIS: Sole species of purported genus.

PALAEOAPTERODYTES AMEGHINO, 1905

Apterodytes AMEGHINO, 1901, p. 81. SIMPSON, 1946, p. 31.

Palaeoapterodytes AMEGHINO, 1905, p. 120. LAMBRECHT, 1933, p. 229. BRODKORB, 1963, p. 236.

ETYMOLOGY: Greek *palaios*, ancient, *a-*, privative prefix, *pteron*, wing, *dytes*, diver, given in the belief that this was a wingless penguin. Ameghino considered *Apterodytes* to be preoccupied by *Apterodyta* Scopoli, 1786, and therefore proposed *Palaeoapterodytes* as a replacement. That is not preoccupation under the present Code, but Brodkorb (1963, p. 236) has pointed out that *Apterodytes* Ameghino, 1891, is in fact preoccupied by *Apterodytes* Hermann, 1783.

TYPE-SPECIES: *P. ictus.*

KNOWN DISTRIBUTION: Patagonia Formation, Patagonia.

AUTHOR'S DIAGNOSIS: Translated from Spanish, "This genus is characterized by the atrophy of the humerus which has become reduced to its proximal part."

DISCUSSION: Lambrecht (1933, pp. 229–230) remarked (here translated from German): "Ameghino believed that the humerus of this form was atrophied in such a way that only the proximal half remained, the distal part of the bone being wholly lost. If this were the case, which is hard to establish without examination of the type in view of Ameghino's many errors, it would be one of the most interesting examples of extreme reversion of the capacity for flight, especially as the presumed atrophy affected only the distal part of the humerus while the proximal continued to be rather strongly developed. According to the illustration, the humerus seems merely to be weathered and the distal half simply broken off."

There cannot be the slightest doubt that Lambrecht's surmise was correct. The bone fragment is heavily abraded, in spite of which the proximal part was clearly normal for a winged penguin — a physical impossibility for a wingless form. Moreover, since penguins swim with their wings, not their feet, a wingless penguin would be unable to swim and would be an inadaptive monstrosity.

I (Simpson, 1946, p. 31) concluded that either Lambrecht's explanation or pathology must be responsible for the evident error. I now think that no pathology was involved, and that this was a normal bone, broken and extensively abraded after death. I concluded that, "The genus is doubtless

technically a synonym of *Palaeospheniscus* or some other from these beds, but synonymy can hardly be established. Based on a manifest error, the name might best be quietly forgotten."

Unfortunately there is no provision in technical nomenclature for quietly forgetting a validly published name, no matter how erroneous or useless it may be zoologically. It can be technically eliminated by rule only if it is a junior homonym or a junior synonym or, under a controversial rule now considered by many to be in obeyance, a *nomen oblitum*. *Apterodytes* is a junior homonym, but *Palaeoapterodytes* is not. Neither qualifies as a *nomen oblitum* even if that rule were recognized. Placing as a synonym would require that the genus be determined, which has not in fact been done. Brodkorb (1963, p. 236) did place both these names in the synonymy of *Palaeospheniscus*, perhaps because I had mentioned that as one possibility among others. In fact it is extremely improbable because on restudy it appears that the sole specimen ever referred to this genus probably did not have a bipartite tricipital fossa, which is always present in *Palaeospheniscus*. There are other possibilities, which I do not specify because I consider *Palaeoapterodytes ictus* really unidentifiable. Fortunately this is not a probable menace to stable nomenclature, because the names most likely to be synonymous are senior to *Palaeoapterodytes* and to *Apterodytes ictus*.

Palaeoapterodytes ictus (Ameghino, 1891)

Apterodytes ictus AMEGHINO, 1901, p. 81. SIMPSON, 1946, p. 31.

Palaeoapterodytes ictus: AMEGHINO, 1905, p. 120, pl. 3, fig. 16 (humerus). LAMBRECHT, 1933, p. 229. BRODKORB, 1963, p. 236 (as synonym of *Palaeospheniscus gracilis*).

ETYMOLOGY: Latin *ictus*, stricken, evidently referring to the belief that the wings had been lost.

HOLOTYPE: MACN (unnumbered), severely abraded proximal part of a humerus, collected by C. Ameghino in the upper Patagonia Formation of the Gulf of San Jorge.

HYPODIGM: The holotype only.

DIAGNOSIS: Not determinable.

DISCUSSION: Although I believe a positive identification to be untenable, the negative conclusion is practically certain that this supposed species is not synonymous with *Palaeospheniscus gracilis*.

TAXA REMOVED FROM THE SPHENISCIDAE

The following taxa are not penguins, but they were originally described and have occasionally been referred to as such. They are therefore listed here with the necessary references and minimal discussion.

ARGYRODYPTES AMEGHINO, 1905

Argyrodyptes AMEGHINO, 1905, p. 121. LAMBRECHT, 1933, p. 230. SIMPSON, 1946, p. 25. BRODKORB, 1963, p. 245.

ETYMOLOGY: Greek *argyros*, silver, *dyptes*, diver; the allusion is evidently to a diving bird occurring in Argentina.

TYPE-SPECIES: *A. microtarsus*, by monotypy and author's designation.

KNOWN DISTRIBUTION: Patagonia Formation, Patagonia.

DIAGNOSIS: Irrelevant here.

DISCUSSION: Lambrecht (1933) apparently had some doubts as to its being a penguin, but concluded that it probably was. I (Simpson, 1946) suggested that it probably was not, and Brodkorb (1963) removed it from the Spheniscidae and placed it in the Procellariidae.

Argyrodyptes microtarsus Ameghino, 1905

Argyrodyptes microtarsus AMEGHINO, 1905, p. 121, pl. 3, fig. 17 (distal part of tibiotarsus), fig. 18 (femur). LAMBRECHT, 1933, p. 230. SIMPSON, 1946, p. 25. BRODKORB, 1963, p. 245.

ETYMOLOGY: Greek *micro-*, small, and *tarsos*, the flat of the foot, here extended to refer to the tibiotarsus, in reference to the slenderness of the latter bone, which would be unique if this bird were a penguin.

SYNTYPES: MACN (unnumbered), distal parts of a tibiotarsus and a femur, supposed to be of one individual, perhaps correctly, collected by C. Ameghino in the lower Patagonia Formation, Rio Seco, San Julián, Santa Cruz.

LECTOTYPE: The tibiotarsus, designated by Brodkorb (1963, p. 245).

KNOWN DISTRIBUTION: Lower Patagonia Formation,[1] Santa Cruz.

DIAGNOSIS: Not relevant here.

CLADORNIS AMEGHINO, 1895

Cladornis AMEGHINO, 1895, p. 584; 1898, p. 230; 1905, p. 151. WIMAN, 1905b, p. 12. LAMBRECHT, 1933, p. 278. SIMPSON, 1946, p. 25. WETMORE, 1930, p. 2. BRODKORB, 1963, p. 264.

ETYMOLOGY: Probably from Greek *klados*, branch, and *ornis*, bird, in reference to its having diverged from other known birds.

TYPE-SPECIES: *C. pachypus*, by monotypy.

KNOWN DISTRIBUTION: Deseadan Stage, Patagonia.

---

[1] Ameghino (1905) placed it as from the "patagónico inferior," which included Ameghino's "Camaronéen" and at least part of his "Juléen" in the French version of his nomenclature (especially 1906). Brodkorb (1963) took this to indicate "Juléen" or, in the Spanish version "Juliense," which is probable. It may, however, be noted that this name is incorrect by present standards. Being derived from Julián, it must become Julianense in Spanish, Julianian in English.

DIAGNOSIS: Not relevant here.

DISCUSSION: Ameghino regularly included this genus in the Impennes (now Sphenisciformes), that is, the penguins in a broad sense, but he considered it unrelated to other groups and put it in a family "Cladornidae," emended by Wetmore to Cladornithidae. At first Ameghino (1895) believed *Cladornis* to be aquatic, but later (1905) he concluded that it was terrestrial. Wiman (1905b) thought it a very primitive, pre-aquatic penguin, and Lambrecht (1933) may have had a doubt, but he quoted Wiman without clear dissent. Thus the legend of a "dry land penguin" arose, and it has gotten into some otherwise excellent accounts of penguins (e.g., Murphy, 1936, p. 334). I (Simpson, 1946, p. 25) rejected any relationship to penguins. Wetmore (1960) put the genus in a suborder Cladornithes of the Pelicaniformes, and this arrangement is accepted by Brodkorb (1963). The myth of the "dry land penguin" should be dropped.

Cladornis pachypus Ameghino, 1895

Cladornis pachypus AMEGHINO, 1895, p. 584, fig. 35 (partial tarsometatarsus); 1898, p. 230; 1905, p. 12, fig. 3 (partial tarsometatarsus). WIMAN, 1905b, p. 12, fig. 2 (after Ameghino, 1895). LAMBRECHT, 1933, p. 238. SIMPSON, 1946, p. 25. BRODKORB, 1963, p. 264.

ETYMOLOGY: Greek *pachys*, heavy, *poys*, foot, suggested by the distal expansion of the tarsometatarsus.

HOLOTYPE: MACN (unnumbered), incomplete distal part of a tarsometatarsus, found by C. Ameghino in the Deseadan Stage ("couches a *Pyrotherium*") of southern Patagonia.

KNOWN DISTRIBUTION: Deseadan, Patagonia.

DIAGNOSIS: Not relevant here.

CRUSCHEDULA AMEGHINO, 1899

Cruschedula AMEGHINO, 1899, p. 9; 1905, p. 154. LAMBRECHT, 1933, p. 238. SIMPSON, 1946, p. 24. BRODKORB, 1964, p. 264.

ETYMOLOGY: Latin *crus*, shin, and *schedula*, a small sheet of paper, because Ameghino believed the only specimen to be a tarsometatarsus flattened into a thin sheet or leaf ("hoja").

TYPE-SPECIES: *C. revola*, by monotypy.

KNOWN DISTRIBUTION: Deseadan Stage, Patagonia.

DIAGNOSIS: Not relevant here.

DISCUSSION: Ameghino (1899) first referred this genus to its own family, Cruschedulidae, but he later put it in the "Cladornidae." Both supposed families were considered Impennes (now Sphenisciformes). Lambrecht (1933) followed Ameghino's second opinion, but I (Simpson, 1946) re-

jected consideration of the genus as a penguin. Although Ameghino had thought that the only known specimen, a small bone fragment, was a tarsometatarsus, Brodkorb (1964) believed it to be the proximal end of a scapula, and he referred the genus to the Accipitridae. It certainly has nothing to do with penguins.

Cruschedula revola Ameghino, 1899

Cruschedula revola AMEGHINO, 1899, p. 9; 1905, p. 154, pl. 8, fig. 40 (supposed tarsometatarsus, probably fragment of scapula, incorrectly referred to as fig. 42 on p. 154). LAMBRECHT, 1933, p. 239. SIMPSON, 1946, p. 24. BRODKORB, 1964, p. 264.

ETYMOLOGY: Origin not clear, but presumably related to Latin *revolare*, to fly back; application also not clear.

HOLOTYPE: MACN (unnumbered), a small bone fragment believed by Ameghino to be part of a tarsometatarsus but by Brodkorb to be part of a scapula, collected by C. Ameghino in the base of the Deseadan stage of the Gulf of San Jorge.

KNOWN DISTRIBUTION: Deseadan, Patagonia.

DIAGNOSIS: Not relevant here.

DISCUSSION OF THE FAUNA AS A WHOLE

In table 3 are listed fossil penguins from various areas. The lists include only taxa believed to be reasonably well established. In each area there are also some dubious taxa that would add to the lists if validated.

In Patagonia the present study recognizes four genera and nine species as well established. They are from a wide area, but all from the Patagonia Formation, and no appreciably different geological ages have been clearly determined. From Seymour Island (Simpson, 1971b) five genera with six species are recognized, all from a small area and of nearly or quite the same geological age although none were found *in situ*. In New Zealand six genera with 10 species are recognized, the largest numbers known from any one region, but they are from at least four or possibly five different stratigraphic stages and from several different localities, although (for identified species) only on the South Island (see Simpson, 1971a). The greatest number unified as to locality and horizon is four genera and five species (one not identified to species) from the Duntroonian of the Waitaki Valley. Only two penguins identifiable to genus or species are known from Australia in the Balcombian or earlier. They differ in both locality and age. A few later fossil penguins are known from Australia, New Zealand, and South Africa, but need not be taken into account here.

The Patagonian assemblage, even without dubious or probably yet undiscovered species, is decidedly the largest known from a comparable

TABLE 3

COMPARATIVE SIZES OF THE MOST CLEARLY IDENTIFIED KNOWN OLDER FOSSIL PENGUINS AND THE LARGEST AND SMALLEST RECENT ANTARCTIC PENGUINS

	Lengths of	
	Tarsometatarsus	Humerus
Patagonia–Patagonia Formation		
Palaeospheniscus gracilis	32	*ca.*70
P. bergi	35	—
P. patagonicus	39	*ca.*75
P. wimani	42½	*ca.*84
Chubutodyptes biloculata	(Larger than *P. wimani*)	
Paraptenodytes antarcticus	53	114
P. robustus	42	91½
?*P. brodkorbi*	—	*ca.*98
Arthrodytes grandis	—	149
Seymour Island–Late Eocene?		
Anthropornis nordenskjoeldii	89	167+
A. grandis	(Slightly larger than *P. gunnari*)	
Palaeeudyptes gunnari	*ca.*65	—
Wimanornis seymourensis	—	133
Archaeospheniscus wimani	*ca.*46	—
Delphinornis larsenii	*ca.*50	—
New Zealand–Late Eocene to late Oligocene		
Palaeeudyptes antarcticus	62	—
P. marplesi	75	—
Pachydyptes ponderosus	—	179
Platydyptes novaezealandiae	—	104
P. amiesi	—	118
?*P. marplesi*	—	95
Archaeospheniscus lowei	—	128
A. lopdelli	55	—
Duntroonornis parvus	*ca.*31	—
Korora oliveri	38	—
Australia–Late Eocene and Middle Miocene		
Palaeeudyptes sp.	—	154
Anthropodyptes gilli	—	*ca.*130
Largest Antarctic Recent penguin		
Aptenodytes forsteri	44	127
Smallest Antarctic Recent penguin		
Pygoscelis adeliae	33	77

area and of a fairly limited geological age, including the Recent. At present along the Antarctic Peninsula and adjacent islands there are three genera and five species, but there is no locality where all are found together except for possible rare strays. In the Falkland or Malvinas Islands there are

regularly four genera and five species, with perhaps an occasional rare stray of another species. There are three genera and five species in the South Sandwich chain, but again rarely if ever at a single locality. I know of no other fairly limited area where as many as five Recent species are found. (For distributions of Recent penguins see Stonehouse, 1967, 1968.)

Of the Patagonian forms, three genera and six species definitely occur together at essentially the same horizon and locality: the basal Patagonia Formation near Gaiman and Trelew. The three species not known to occur there, *Paraptenodytes robustus*, ?*Paraptenodytes brodkorbi*, and *Arthrodytes grandis*, are rare, known from only one or two specimens each, so that the negative evidence is not impressive. It seems definite that in the mid-Tertiary penguins were more varied in Patagonia than they are any place today. That was quite probably true also of some other times and areas, such as the Duntroonian of New Zealand's South Island, where sampling has been less intensive and collections are smaller.

None of the known Patagonian species and probably none of the genera are known from anywhere else. The only possible exception is that *Korora oliveri*, from the Waitakian of New Zealand, resembles *Palaeospheniscus* and is somewhat doubtfully separable generically. It is significant that it is probably closer to the Patagonian fauna in age than other known New Zealand species. In contrast, the Seymour Island fauna, as now revised (Simpson, 1971b) has two of its five genera in common with late Eocene — early Oligocene genera of New Zealand, and the other three also have fairly close relatives in New Zealand. Although it was long believed that the Seymour Island fauna was of nearly or quite the same age as the Patagonian, it now appears that the former is significantly older, probably late Eocene or thereabouts.

In addition to the taxonomic differences, which can be ascribed at least in part to differences in age, it appears that the Patagonian fossil penguin fauna was ecologically different from that of Seymour Island or the older faunas of New Zealand, whereas the last two were generally similar to each other in this respect. This is reflected in the sizes of the included species, indicated in table 3 by lengths of tarsometatarsi and humeri. It is seen that only two of the nine Patagonian species were larger than the smallest Seymour Island species. Such differences are doubtless unduly influenced by vagaries of preservation and collecting, but the collections support the impressions, first, that the earlier faunas of Seymour Island and New Zealand included much larger species, and second, that the commonest species in Patagonia were of moderate size, more or less comparable to such modest forms as the Magellanic penguins still so common in Patagonia, whereas at Seymour Island and New Zealand the commonest

species were notably larger than any living anywhere today.

There is some independent evidence that the climate in Patagonia around the time of these fossil penguins became milder than it is now. For example, ceboid monkeys, a group mainly tropical in Recent distribution and nowhere cold temperate, had been present farther north in South America since at least the Deseadan, but they appeared in Patagonia only just before the Patagonian marine incursion and disappeared from there (became confined to warmer, more northern areas) soon thereafter. The size of penguins does now correlate rather loosely in an inverse way with water temperature, but there are reasons to believe that the correlation was quite different in the early to middle Tertiary (see Simpson, 1971a).

It must be remembered that *Arthrodytes grandis*, a penguin much larger than the Recent emperor, was living (or at least, dying) in Patagonia during what seems to have been an unusually warm episode. Although, as noted above, the negative evidence does not have much force, it is true that this largest known Patagonian species is from one of the southernmost localities, San Julián, and that the three species not definitely known from northern localities (in Chubut), *Arthrodytes grandis*, ?*Paraptenodytes brodkorbi*, and *Paraptenodytes robustus* are all larger than the most common northern species. It is also true that the smallest known species, *Palaeospheniscus gracilis*, is so far definitely recorded only from Chubut and not from the more southern localities in Santa Cruz.

It is thus possible to speculate that some latitudinal zoning by size occurred, but the apparent effect could just as well be the result of mere chances of preservation and recovery. All the fossil localities are far within the latitudinal range of single species (e.g., *Spheniscus magellanicus*) today, but there are also several Recent species, among them the large *Aptenodytes patagonicus*,[1] that nearly reach the latitude of the southern but never reach anywhere near that of the northern fossil localities. The present latitude of Trelew is 43° 13′ south and that of San Julián is 49° 17′ south. The latitudes may not have been exactly the same at the beginning of the Miocene, but the difference between them has probably not changed significantly.

LITERATURE CITED

AMEGHINO, F.
1891. Enumeración de las aves fósiles de la República Argentina. Rev.

[1] This name is usually still written *A. patagonica*, but as Murphy (1936) had already noted, A. *patagonicus* is correct.

Argentina Hist. Nat., vol. 1, pt. 6a, pp. 441–445.

1895. Sur les oiseaux fossiles de Patagonie. Bol. Inst. Geogr. Argentina, vol. 15, pp. 501–602.

1898. Sinopsis geológico-paleontológica. *In* Fuente, Diego de la, (ed.), Segundo censo de la República Argentina. Buenos Aires, Taller Tipográfico de la Penitenciaría Nacional, vol. 1, pt. 3, pp. 111–255, 105 figs.

1899. Sinopsis geológico-paleontológica. Suplemento. La Plata, La Libertad, pp. 1–13.

1901. L'âge des formations sédimentaires de Patagonie. An. Soc. Cien. Argentina, vol. 51, pp. 20–39, 65–91.

1905. Enumeración de los impennes fósiles de Patagonia y de la Isla Seymour. An. Mus. Nac. Buenos Aires, ser. 3, vol. 6, pp. 97–167, 4 figs., 8 pls.

1906. Les formations sédimentaires du Crétacé supérieur et du Tertiaire de Patagonie. *Ibid.*, ser. 3, vol. 8, pp. 1–568.

1934. Enumeración de los impennes fósiles de Patagonia y de la Isla Seymour. *In* Torcelli, A. J., (ed.), Obras completas y correspondencia científica de Florentino Ameghino. La Plata, Impresiones Oficiales, vol. 15, pp. 511–576, 4 figs., 8 pls.

BRODKORB, P.

1963. Catalogue of fossil birds. Part 1 (Archaeopterygiformes through Ardeiformes). Bull. Florida State Mus., Biol. Sci., vol. 7, no. 4, pp. 179–293.

1964. Catalogue of fossil birds. Part 2 (Anseriformes through Galliformes). *Ibid.*, vol. 8, no. 3, pp. 195–335.

FERUGLIO, E.

1949–1950. Descripción geológica de la Patagonia. Buenos Aires, Dir. Gen. Yacimientos Petrolíferos Fiscales, vol. 1, xv + 334 pp., vol. 2, 349 pp., vol. 3, 431 pp.

LAMBRECHT, K.

1933. Handbuch der Palaeornithologie. Berlin, Gebrüder Borntraeger, xix + 457 pp., 209 figs., 4 tables.

LOOMIS, F. B.

1914. The Deseado Formation of Patagonia. Eighth Amherst Expedition 1911. Amherst College, Amherst, 232 pp., 160 figs.

LOWE, P. R.

1933. On the primitive characters of the penguins and their bearing on the phylogeny of birds. Proc. Zool. Soc. London, pt. 2, pp. 483–538.

1939. Some additional notes on Miocene penguins in relation to their origin and systematics. Ibis, ser. 14, vol. 3, pp. 281–294.

MORENO, F. P., AND A. MERCERAT

1891. Catálogo de los pájaros fósiles de la República Argentine conservados en el Museo de La Plata. An. Mus. La Plata, Paleont. Argentina, vol. 1, pp. 8–71, 21 pls.

MURPHY, R. C.

1936. Oceanic birds of South America. New York, the American Museum of Natural History, vol. 1, xxii + 640 pp., vol. 2, pp. 641–1245.

SAEZ, MATHILDE DOLGOPOL DE

1927. Una curiosa relación constante en el esqueleto apendicular de los esfeniscidos. Hornero, IV, pp. 77–78.

SIMPSON, G. G.
1935. Early and middle Tertiary geology of the Gaiman region, Chubut, Argentina. Amer. Mus. Novitates, no. 775, pp. 1–29.
1946. Fossil penguins. Bull. Amer. Mus. Nat. Hist., vol. 87, art. 1, pp. 7–99, 9 tables.
1962. Notes on the names of some Argentine fossil mammals. Rev. Mus. Argentino Cien. Nat., Cien. Zool., vol. 8, no. 2, pp. 15–26.
1967. The Ameghinos' localities for early Cenozoic mammals in Patagonia. Bull. Mus. Comp. Zool., vol. 136, no. 4, pp. 63–76, 3 figs.
1970. Miocene penguins from Victoria, Australia, and Chubut, Argentina. Mem. Nat. Mus. Victoria, vol. 31, pp. 17–24.
1971a. A review of the pre-Pliocene penguins of New Zealand. Bull. Amer. Mus. Nat. Hist., vol. 144, art. 5, pp. 319–378.
1971b. A review of fossil penguins from Seymour Island. Proc. Roy. Soc. London, B, vol. 178, pp. 357–387.
STOLL, N. R., AND OTHERS
1961. International code of zoological nomenclature. London, Internatl. Trust for Zoological Nomenclature, London, 176 pp.
STONEHOUSE, B.
1967. The general biology and thermal balances of penguins. Adv. Ecol. Res., vol. 4, pp. 131–196.
1968. Penguins. New York, Golden Press.
WETMORE, A.
1930. A systematic classification for the birds of the world. Proc. U. S. Natl. Mus., vol. 76, art. 24, pp. 1–8.
1960. A classification for the birds of the world. Smithsonian Misc. Coll., vol. 139, no. 11, pp. 1–37.
WIMAN, C.
1905a. Vorläufige Mitteilung über die alttertiären Vertebraten der Seymourinsel. Bull. Geol. Inst. Univ. Uppsala, vol. 6, nos. 11–12 (for 1902–1903), pp. 247–253, pl. 12.
1905b. Die alttertiären Vertebraten der Seymour-Insel. *In* Nordenskjöld, Nils Otto, (ed.), Wissenschaftliche Ergebnisse der Schwedischen Südpolar-Expedition 1901–1903. Stockholm, P. A. Norstedt & Söner, vol. 3, art. 1, pp. 1–37, 8 tables.